

A NEW EXTINCT SPECIES OF *SOLENODON*
(MAMMALIA: INSECTIVORA: SOLENODONTIDAE)
FROM THE LATE QUATERNARY OF CUBA

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ABSTRACT

An extinct species of giant *Solenodon*, *S. arredondo*, is described on the basis of a partial skull and a small sample of postcranial elements from three Late Quaternary fossil deposits in western Cuba. *S. arredondo* can be distinguished from all other species of *Solenodon* by its considerably larger size. Cranial features in which *S. arredondo* differs from the two Hispaniolan species of *Solenodon*, the living *S. paradoxus* and the extinct *S. marcanoi*, include the absence of an os proboscis, relatively broader frontals at the anterior edge of the orbits, more pronounced interorbital constriction, constricted internal narial opening and anterior portion of pterygoid fossa, and much larger posteroventrally expanded pterygoid processes. Dental characters separating *S. arredondo* from *S. paradoxus* are the greatly enlarged and inflated C¹, lack of accessory cusps on C¹, and presence of a noticeable diastema between I³ and C¹. *S. arredondo* is closely related to the living Cuban *Solenodon*, *S. cubanus*, but differs from that species in its larger size, as well as the somewhat more constricted interorbital region, narrower internal narial opening, more prominent pterygoid processes, comparatively more inflated C¹, and broader upper molars. The diverse fauna of extinct birds and mammals collected in association with *S. arredondo* indicates a Late Quaternary age (late Pleistocene or early Holocene) for this species. The giant Cuban *Solenodon* is one of the largest known members of the order Insectivora, living or extinct. It was probably carnivorous, preying on larger invertebrates and a variety of small to medium-sized terrestrial vertebrates.

INTRODUCTION

The existence of a very large extinct species of *Solenodon* from Cuba was first mentioned by Arredondo (1970) based on a femur he collected 16 years earlier from a fossil deposit at Abra de Andrés, in the Sierra de Anafe, La Habana Province, western Cuba. This femur was later figured and described in detail by Morgan et al. (1980). These authors also mentioned the existence of two other large fossil femora of *Solenodon* from western Cuba, one each from Caverna de Pío Domingo, Pinar del Río Province and Cueva Paredones, La Habana Province. Both of these specimens were intermediate in size between the extremely large fossil femur from Abra de Andrés and the living Cuban species, *Solenodon cubanus* Peters. Morgan et al. (1980) did not name a new species because they felt that a single incomplete femur was an inadequate element upon which to describe a new taxon. In early 1991, while examining specimens in the Museo Nacional de Historia Natural in La Habana, Cuba, Oscar Arredondo discovered a partial skull

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Table 1.—Cranial measurements of fossil and Recent *Solenodon* from Cuba. Statistics for the samples of fossil and Recent *S. cubanus* are (in order) mean, standard deviation (± 1 SD), observed range, coefficient of variation, and sample size (N).

Species and locality	Antorbital constriction	Zygomatic breadth	Interorbital constriction	Squamosal breadth	Palatal length	Palatal breadth	Alveolar length of maxillary toothrow
<i>Solenodon arredondo</i> (type)							
Cueva Paredones MNHNC 421/123	19.0	39.0	16.3	35.4	40.7	25.2	28.0
<i>Solenodon cubanus</i> (fossil)	17.1 \pm 0.5	34.3 \pm 0.6	15.7 \pm 0.7	31.2	35.7 \pm 1.6	23.7 \pm 0.8	25.2 \pm 0.6
	16.8–17.8	34.0–35.0	15.3–16.2	—	33.9–37.2	22.9–24.3	24.5–26.0
	3.3 N = 3	1.7 N = 3	4.1 N = 2	— N = 1	4.4 N = 4	3.2 N = 3	2.5 N = 4
<i>Solenodon cubanus</i> (Recent)	15.0 \pm 0.7	32.4 \pm 1.3	15.2 \pm 0.6	30.9 \pm 0.8	34.3 \pm 1.1	21.5 \pm 1.2	23.7 \pm 0.9
	14.3–16.4	30.5–35.2	14.5–16.4	29.6–31.9	31.8–35.7	20.3–23.9	21.8–24.7
	4.8 N = 14	4.0 N = 9	4.1 N = 13	2.6 N = 12	3.1 N = 14	5.4 N = 14	3.7 N = 14

of a very large *Solenodon* from a fossil deposit in Cueva Paredones. The discovery of this skull permits a thorough description of the previously unnamed giant *Solenodon*. We have also re-examined and measured the three large *Solenodon* femora mentioned in the literature, as well as several additional cranial and postcranial elements that pertain to this new species.

Comparisons and measurements of the *Solenodon* skull from Cueva Paredones reveal that this specimen, like the femur from Abra de Andrés reported by Arredondo (1970) and Morgan et al. (1980), is considerably larger than either of the two extant species of *Solenodon*, *S. cubanus* Peters from Cuba and *S. paradoxus* Brandt from Hispaniola. We present a morphological description and measurements (Tables 1–4) of this new large *Solenodon*, as well as comparisons with the two living and one other extinct species in the genus, *S. marcanoi* Patterson from Hispaniola. The *Solenodon* fossils from western Cuba described here belong to a new species that is not only much larger than any previously described member of the genus, but is also one of the largest known species in the order Insectivora.

METHODS AND ABBREVIATIONS

Explanations of the cranial characters and measurements of *Solenodon* used herein are presented by Ottenwalder (1991). Excellent descriptions and illustrations of the cranial anatomy and dentition of *Solenodon* have been published by McDowell (1958). We follow the standardized dental nomenclature for mammals (e.g., Szalay, 1969). However, the cusp homologies of the upper molars and the molariform P^4 of *Solenodon* are in question. In attempting to demonstrate a close phylogenetic relationship between *Nesophontes* and *Solenodon*, McDowell (1958) interpreted the large central cusp on the P^4 – M^3 of *Solenodon* to be the protocone. He also proposed that the metacone on these teeth was lost and that the paracone was represented by a tiny cusp located on the paracrista anterolabial to the protocone. However, most other authors (Butler, 1937, 1939; Van Valen, 1966, 1967; Hershkovitz, 1971) considered the primary cusp on the upper molariform teeth of *Solenodon* to be the paracone. According to these workers, a metacone is absent and the two cusps on the lingual cingulum are the slightly larger anterolingual protocone and the smaller posterolingual hypocone. We follow the latter dental terminology for *Solenodon* molariform teeth, as it appears to be the most commonly accepted and the least controversial. It should also be noted that mammalian paleontologists have long disagreed on the origin and homology of the central cusp in zalambdodont molars, such as those of *Solenodon*.

There is also some disagreement among previous authors on the dental formula of *Solenodon*, which lacks one tooth in each jaw quadrant compared to the primitive eutherian dentition. The missing tooth is obviously a premolar, but it is unclear whether this is the $P^{2/2}$ or $P^{3/3}$. We follow McDowell (1958) who tentatively regarded the missing premolars as the $P^{3/3}$.

Poduschka and Poduschka (1983) examined the external, cranial, and dental characters used by previous workers to distinguish *Solenodon cubanus* from *S. paradoxus*. In particular, they evaluated the validity of the genus *Atopogale*, established by Cabrera (1925) for *S. cubanus*. It is not our intent to comment extensively on the relationship between *S. cubanus* and *S. paradoxus*, as a thorough systematic review of the genus *Solenodon* has already been undertaken (Ottenwalder, 1991). Our discussion and comparisons are primarily limited to characters that can be observed in the fossil material of the new species of *Solenodon* from Cuba.

The following museums, institutions, and collections possess specimens of Recent and fossil *Solenodon* examined during this study. The abbreviations used in this paper for each of these collections are as follows: Instituto de Ecología y Sistemática, Academia de Ciencias de Cuba, Havana, Cuba (IES/ACC); Jose A. Ottenwalder, private field collections, Santo Domingo, Dominican Republic (JAO); Museum of Comparative Zoology, Harvard University (MCZ); Museo Nacional de Historia Natural de Cuba, Havana, Cuba (MNHNC); Personal collection of Oscar Arredondo, Havana, Cuba (OA); Florida Museum of Natural History, University of Florida (UF); United States National Museum of Natural History, Smithsonian Institution (USNM).

Table 2.—Measurements of upper teeth of fossil and Recent *Solenodon* from Cuba. Statistics for samples of fossil and Recent *S. cubanus* are (in order) mean, standard deviation (± 1 SD), observed range, coefficient of variation, and sample size (N).

Species and locality	Length M ¹ –M ³	Length C ₁	Width C ₁	Length P ¹	Width P ¹	Length P ²
<i>Solenodon arredondo</i> (type)						
Cueva Paredones						
MNHNC 421/123	9.7	6.2	4.0	4.0	2.9	5.2
<i>Solenodon cubanus</i>						
(fossil)	—	4.6 \pm 0.2	3.1 \pm 0.1	3.4 \pm 0.2	2.3 \pm 0.1	3.8 \pm 0.6
	—	4.4–4.8	3.0–3.2	3.2–3.7	2.2–2.4	3.4–4.6
	—	4.7	4.2	6.1	5.1	16.2
	—	N = 3	N = 3	N = 4	N = 4	N = 3
<i>Solenodon cubanus</i>						
(Recent)	8.6 \pm 0.4	4.5 \pm 0.3	3.0 \pm 0.2	3.1 \pm 0.1	2.4 \pm 0.1	3.8 \pm 0.4
	8.0–9.6	4.1–4.8	2.6–3.2	2.9–3.2	2.4–2.5	3.1–4.2
	5.1	6.1	5.7	3.5	2.1	11.6
	N = 12	N = 12	N = 12	N = 5	N = 5	N = 5

SYSTEMATIC PALEONTOLOGY

Order Insectivora Bowdich, 1821
 Suborder Soricomorpha Saban, 1954
 Family Solenodontidae Dobson, 1882
 Genus *Solenodon* Brandt, 1833
Solenodon arredondo, new species
 (Fig. 1)

Holotype.—MNHNC 421/123, nearly complete skull lacking only the braincase, with right M¹ and M³ and left C¹, P¹, P², M¹, M². Cueva Paredones, 3 km southwest of Ceiba del Agua, San Antonio de los Baños, La Habana Province, Cuba.

Referred specimens.—Additional fossils from type locality (Cueva Paredones): IES/ACC P-2431/3675, edentulous palatal fragment; IES/ACC uncatalogued, partial braincase, including parietals and occipitals; IES/ACC 278, complete right humerus; MNHNC uncatalogued, right proximal humerus, collected by Manuel Iturralde in April 1991; OA 2943, right femur missing distal end, collected by Oscar Arredondo in September 1959 (Morgan et al., 1980).

USNM 299480, partial left femur from Abra de Andrés, Altura del Esperón, Sierra de Anafe, northeast of Guanajay, La Habana Province, Cuba. Collected by Oscar Arredondo and César García del Pino on 15 March 1959 (Arredondo, 1970; Morgan et al., 1980). As noted by Morgan et al. (1980), this locality was actually in Pinar del Río Province when the specimen was collected, prior to the reorganization of the Cuban provincial boundaries. Under the new geographic subdivision the boundary between the provinces of Habana and Pinar del Río was moved to the west and Guanajay and environs are now in Habana Province.

OA 301E, partial associated skeleton, including: left humerus, right radius, left ulna, right innominate, left femur, right proximal and left distal tibia, and left calcaneum from Caverna de Pío Domingo, Ensenada Pica-Pica, Sierra de Sumidero, Pinar del Río Province, Cuba. Collected by Oscar Arredondo and J. N. Otero, January 1954 (Arredondo, 1955; Morgan et al., 1980).

Diagnosis.—*Solenodon arredondo* can be distinguished from all other species in the genus *Solenodon* by its considerably larger size. *S. arredondo* differs from the two Hispaniolan species, *S. paradoxus* and *S. marcanoi*, in the absence of an os proboscis, the relatively broader frontals at the anterior edge of the orbits, more pronounced interorbital constriction, constricted internal narial opening and anterior portion of pterygoid fossa, much larger posteroventrally expanded pterygoid processes, and greatly enlarged and inflated C¹. Additional characters separating *S. arredondo* from *S. paradoxus* include the presence of a diastema

Table 2.—*Extended.*

Width P ²	Length M ¹	Width M ¹	Length M ²	Width M ²	Length M ³	Width M ³
4.2	4.5	7.5	3.3	7.3	2.2	5.8
3.8 ± 0.8	4.0 ± 0.5	6.5 ± 0.1	3.2	5.8	—	—
3.8–3.9	3.5–4.6	6.3–6.6	—	—	—	—
2.0	11.2	1.9	—	—	—	—
N = 3	N = 4	N = 4	N = 1	N = 1		
3.7 ± 0.3	3.5 ± 0.3	6.7 ± 0.4	2.6 ± 0.3	6.1 ± 0.3	2.0 ± 0.1	4.7 ± 0.3
3.3–3.9	3.2–4.0	6.1–7.4	2.0–3.0	5.7–6.8	1.8–2.3	4.2–5.3
7.1	7.3	6.3	12.5	5.5	6.6	6.6
N = 5	N = 11	N = 11	N = 11	N = 11	N = 11	N = 12

between I³ and C¹ as well as smaller but distinct diastemata between I² and I³ and C¹ and P¹, strong lingual expansion of P², and lack of anterior accessory cusps on C¹, P¹, and P². Besides its larger size, *S. arredondo* can be distinguished from the other Cuban species *S. cubanus* by its somewhat more constricted interorbital region, narrower internal narial opening, more prominent pterygoid processes, comparatively more inflated C¹, and broader upper molars.

Description and comparisons.—Although the skulls of *Solenodon arredondo*, *S. cubanus*, *S. marcanoi*, and *S. paradoxus* are generally similar overall, there are numerous morphological features that distinguish the four species. As would be predicted on the basis of geography, *S. arredondo* is more similar to *S. cubanus* than to the two Hispaniolan species in the genus, *S. paradoxus* and *S. marcanoi*. Only characters that can be observed in the type specimen and referred material of *S. arredondo* are discussed here. More detailed morphological and mensural comparisons of *S. cubanus*, *S. paradoxus*, and *S. marcanoi* are presented by Ottenwalder (1991).

Table 3.—*Measurements of the humerus of fossil and Recent Solenodon from Cuba. Statistics for the sample of Recent S. cubanus are (in order) mean, standard deviation (± 1 SD), observed range, and coefficient of variation.*

Species and locality	Total length	Proximal breadth	Proximal depth	Minimum shaft width	Distal breadth
<i>Solenodon arredondo</i>					
Cueva Paredones					
P-278	56.3	13.5	13.0	5.2	20.0
uncatalogued	—	12.6	12.1	4.8	—
<i>Solenodon arredondo</i>					
Caverna de Pío Domingo					
OA 301E	51.7	12.4	12.3	4.8	18.9
<i>Solenodon cubanus</i> (fossil)					
Cueva Paredones					
IES/ACC P-621	44.3	10.9	9.9	4.2	15.3
<i>Solenodon cubanus</i> (Recent)					
N = 5	43.0 ± 1.3	10.3 ± 0.5	9.7 ± 0.3	3.8 ± 0.1	14.7 ± 0.7
	41.6 ± 44.7	10.0–11.0	9.4–9.9	3.7–4.0	14.2–15.9
	3.02	4.44	2.98	3.00	4.65

Table 4.—Measurements of the femur of fossil and Recent *Solenodon* from Cuba. Statistics for the sample of Recent *S. cubanus* are (in order) mean, standard deviation (± 1 SD), observed range, and coefficient of variation.

Species and locality	Total length	Proximal breadth	Diameter of head	Width at third trochanter	Minimum shaft width	Distal breadth	Distal depth
<i>Solenodon arredondo</i>							
Abra de Andrés USNM 299480	66.1	—	—	11.6	7.1	—	14.4
<i>Solenodon arredondo</i>							
Caverna de Pio Domingo OA 301E	57.8	16.4	8.3	10.5	6.2	14.4	12.7
<i>Solenodon arredondo</i>							
Cueva Paredones OA 2943	—	16.2	8.0	9.2	6.4	—	—
<i>Solenodon cubanus</i> (fossil)							
Cueva Paredones IES/ACC P-620	48.2	13.3	6.8	6.7	5.1	12.2	9.4
IES/ACC P-2599	—	14.1	6.4	7.3	5.1	—	—
<i>Solenodon cubanus</i> (Recent) N = 5	46.8 \pm 0.9	12.9 \pm 0.5	6.7 \pm 0.3	7.6 \pm 0.7	4.5 \pm 0.2	11.7 \pm 0.7	10.1 (N = 1)
	45.6–47.9	12.3–13.5	6.3–7.0	6.9–8.6	4.2–4.6	11.0–12.7	—
	1.87	3.81	4.65	8.80	3.85	5.82	—

The most important characters of the skull and upper dentition common to *S. arredondo* and *S. cubanus*, and that separate them from *S. paradoxus* and *S. marcano*, include the more constricted internal narial opening, expanded pterygoid processes, lack of an os proboscis, and noticeably inflated C^1 . In addition to these differences, *S. arredondo* is characterized by its very large size compared to all other members of the genus (see measurements in tables 1–4). Detailed comparisons of *S. arredondo* will be made primarily with the two living species of *Solenodon*, *S. cubanus* and *S. paradoxus*.

Until recently, the smallest member of the genus *Solenodon*, *S. marcano*, an extinct species from Hispaniola, was known only from the type mandible and several postcranial elements (Patterson, 1962). Patterson originally placed *S. marcano* in the monotypic genus *Antillogale*, which was later synonymized with *Solenodon* by Van Valen (1967). Extensive new material of *S. marcano* from fossil deposits in southern Haiti, including the first known skulls, has been described elsewhere by Ottenwalder (1991). In addition to the morphological differences mentioned above, *S. arredondo* is so much larger than *S. marcano* that further comparisons are unnecessary.

Perhaps the most prominent differences among the species of *Solenodon* are in the pterygoid region. The opening for the internal nares posterior and dorsal to the palate is much smaller and more compressed in *S. arredondo* and *S. cubanus* than in *S. paradoxus*. The anterior portion of the pterygoid fossa is also much narrower in the two Cuban species, but is markedly broader posteriorly at the level of the postglenoid processes. In most specimens of *S. paradoxus*, the pterygoid fossa is broadest anteriorly at the posterior edge of the palate and then becomes slightly narrower posteriorly, although in some skulls the pterygoid fossa is essentially parallel-sided. The pterygoid processes are much larger and better developed in *S. arredondo* and *S. cubanus* than in *S. paradoxus*. The pterygoid processes form a high, thin wall for the pterygoid fossa in the two Cuban species, extending ventrally and posteriorly to about the same level as the postglenoid processes. The reduced pterygoid processes of *S. paradoxus* do not extend nearly as far posteroventrally.

Solenodon arredondo and *S. cubanus* both possess a more noticeable interorbital (=postorbital) constriction than does *S. paradoxus*. This feature is related not only to the deeper constriction in the two Cuban species, but also to the fact that their frontals are relatively broader and more inflated in the region between the anterior edge of the orbits and the postorbital constriction. Thus, the frontals are distinctly broader at the anterior edge of the orbits in *S. arredondo* and *S. cubanus* and become narrower posteriorly to the level of the strong interorbital constriction. The frontals are almost parallel-sided in *S. paradoxus* in dorsal aspect and the interorbital constriction is not as prominent.

The os proboscis (=paranasal or prenasal bone) is present in all specimens of *Solenodon paradoxus*, both adult and juvenile, but is absent in *S. cubanus* (Ottenwalder, 1991). In *S. paradoxus*, the anterior edge of the premaxilla dorsal to the I^1 possesses a small concavity or invagination where the os proboscis articulates. There is no articular facet for the os proboscis in *S. cubanus*, and the anterior edge of the premaxilla is squared off and projects somewhat anteriorly. The anterior portion of the premaxilla in the type skull of *S. arredondo* has the same morphology as does *S. cubanus*, indicating that an os proboscis was absent (Ottenwalder, 1991).

The primary dental differences between *Solenodon arredondo* and *S. cubanus* on the one hand and *S. paradoxus* on the other are in the canines and premolars. In general, the upper canines and first two upper premolars are noticeably broader and more inflated in the two Cuban species than in the Hispaniolan species. These teeth are more laterally (buccolingually) compressed in *S. paradoxus*. Conversely, the upper molariform teeth (P^4 – M^3) of *S. paradoxus* are larger than those of *S. cubanus*. Consequently, *S. cubanus* has a comparatively larger antemolar dentition and smaller molars than does *S. paradoxus*. These same dental relationships hold true for *S. arredondo*, as the upper canine and premolars of this species are greatly enlarged compared to *S. paradoxus*. The molars are about the same size in the two species even though *S. arredondo* is considerably larger in all other cranial dimensions (see complete comparisons and measurements in Ottenwalder, 1991).

Another dental difference between the Cuban species and *S. paradoxus* is the presence of a well-developed diastema between I^3 and C^1 in *S. arredondo* and *S. cubanus* and the lack of this diastema in most specimens of *S. paradoxus*. Some skulls of *S. paradoxus* examined do have a slight diastema between these two teeth, but it is never as well developed as in *S. cubanus* or *S. arredondo*. The two Cuban species of *Solenodon* also have short, but distinct, diastemata between I^2 and I^3 and between C^1 and P^1 , both of which are totally absent in *S. paradoxus*.

The most distinctive tooth of *Solenodon arredondo* and *S. cubanus* is the upper canine. The upper canine of the two Cuban species is much larger than the C^1 of *S. paradoxus*, being strongly inflated, especially in the buccolingual dimension. The C^1 of *S. cubanus* is similar in anteroposterior length to the C^1 of *S. paradoxus*, but is much broader, whereas the C^1 of *S. arredondo* is far larger than that of any other *Solenodon*. Furthermore, probably because of its inflation, the C^1 of *S. arredondo* and *S. cubanus* lacks any evidence of accessory cusps. *S. paradoxus* possesses distinct accessory cusps at the base of the crown on both the anterior and posterior edges of the C^1 . The presence of the anterior

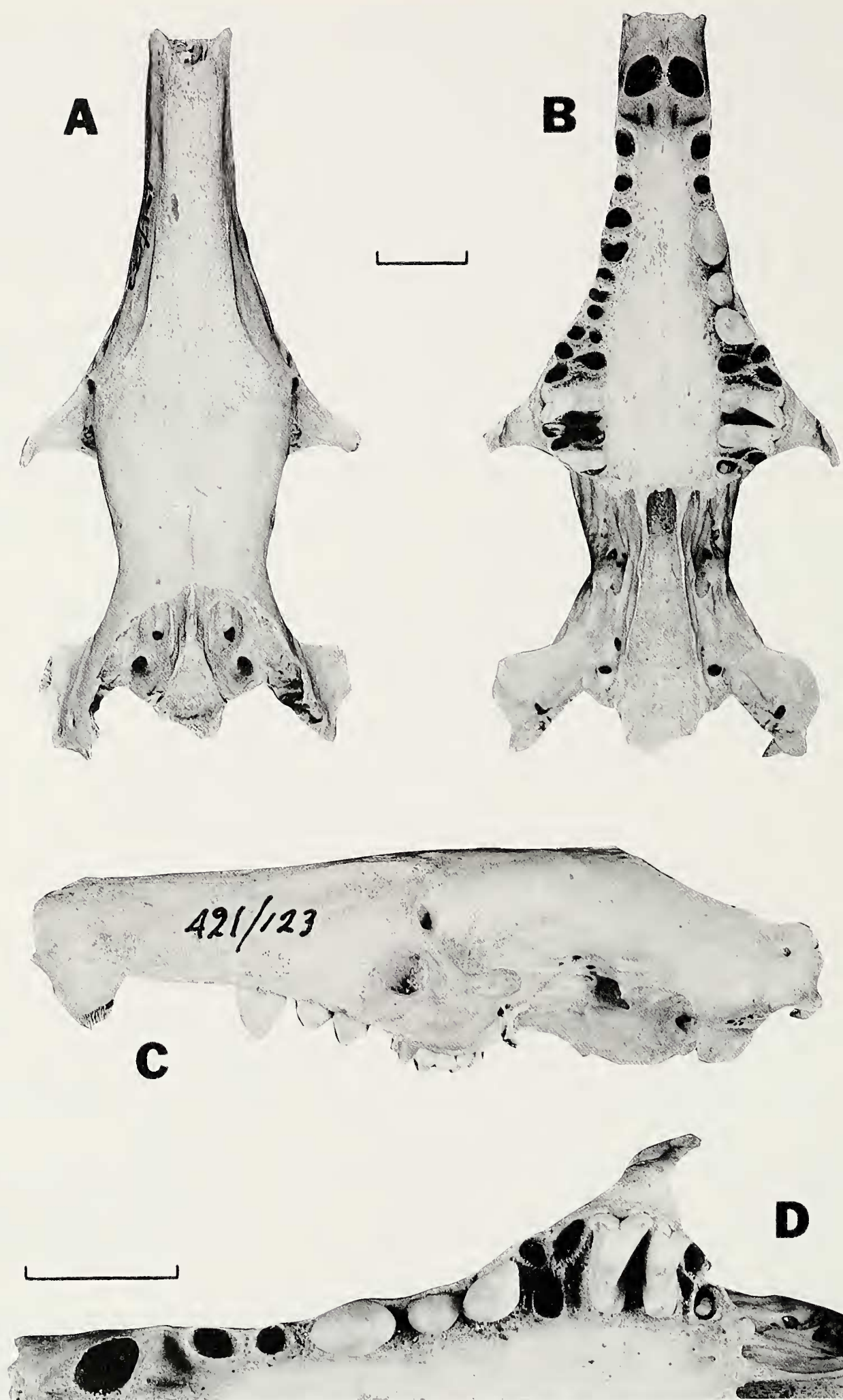


Fig. 1.—Photographs of the holotype skull (MNHNC 421/123) of *Solenodon arredondoii* from Cueva Paredones, La Habana Province, Cuba in dorsal (A), ventral (B, D), and left lateral (C) views. Both scale bars represent 10 mm; the top scale applies to A–C, the bottom scale applies to D.

accessory cusp on the C^1 of *S. paradoxus* has been regarded as one of the most important dental characters distinguishing this species from *S. cubanus* (e.g., Poduschka and Poduschka, 1983). The inflation of the C^1 in *S. arredondo*i and *S. cubanus* and the overall difference in size and shape of this tooth between the two Cuban species of *Solenodon* and *S. paradoxus* seem to be much more diagnostic features than are the accessory cusps.

The type skull of *Solenodon arredondo*i and specimens of *S. cubanus*, both Recent and fossil, also lack anterior accessory cusps on P^1 and P^2 . The C^1 , P^1 , and P^2 all possess anterior accessory cusps in *S. paradoxus*. The P^1 of the two Cuban species is also somewhat inflated in the buccolingual dimension compared to *S. paradoxus*. The P^2 of *S. arredondo*i and *S. cubanus* is relatively large owing to a posterolingual expansion of the tooth, giving it a rounded triangular occlusal outline. The P^2 of *S. paradoxus* generally lacks this lingual expansion, and thus has a narrower more elongated occlusal outline like the C^1 and P^1 . Several specimens of *S. paradoxus* examined had a somewhat triangular-shaped P^2 ; however, this tooth was considerably smaller and less inflated than the P^2 in the two Cuban species. The P^4 of *S. cubanus* also appears to differ in several important features from that of *S. paradoxus*. The P^4 of *S. cubanus* has a more reduced parastyle, a nearly straight labial margin essentially lacking any evidence of an emargination, and a smaller hypocone. The P^4 is not present in the type of *S. arredondo*i. Like the P^4 , the M^1 and M^2 of *S. arredondo*i and *S. cubanus* also have a more reduced hypocone than does *S. paradoxus*.

The most important difference between the two Cuban species of *Solenodon* is obviously the much larger size of *S. arredondo*i compared to *S. cubanus* (tables 1–4). However, there are several other cranial and dental characters that distinguish these two species as well. The internal narial opening in the type skull of *S. arredondo*i is even more constricted than in *S. cubanus*, as is the anterior portion of the pterygoid fossa. The pterygoid processes are also better developed in the larger species, projecting somewhat farther ventrally and posteriorly than in *S. cubanus*. The two Cuban species of *Solenodon* are much more similar to one another in features of the internal nares, pterygoid fossa, and pterygoid processes than either is to *S. paradoxus*. The interorbital constriction in the type skull of *S. arredondo*i is more prominent than in any of the skulls of *S. cubanus* examined. The C^1 is relatively larger and more inflated in *S. arredondo*i than in *S. cubanus*. The M^1 and M^2 in the two Cuban species are similar in anteroposterior length (Table 2); however, these teeth are much broader in *S. arredondo*i giving them a more elongated shape than in *S. cubanus*.

Morgan et al. (1980) described the three femora here referred to *Solenodon arredondo*i. Additional postcranial elements attributed to *S. arredondo*i include a complete and a proximal humerus from Cueva Paredones and a partial skeleton from Caverna de Pío Domingo. All of the available limb bones of *S. arredondo*i are larger than those of the two extant species of *Solenodon* (see measurements of humeri and femora in tables 3 and 4). Although the sample size is quite small, there does appear to be some variation in the size of the postcranial elements referred to *S. arredondo*i. Two of the three femora of *S. arredondo*i, one from Caverna de Pío Domingo (OA 301E) and one from Cueva Paredones (OA 2943), were tentatively identified as *S. cubanus* by Morgan et al. (1980), although they stated that both of these specimens were substantially larger than the single modern femur of *S. cubanus* available to them for study (USNM 49508). Only the extremely large femur from Abra de Andrés (USNM 299480) was considered by these authors to belong to the giant *Solenodon*. We follow Ottenwalder (1991) in referring the two intermediate-sized femora to *S. arredondo*i.

We examined and measured five modern skeletons of *S. cubanus* (tables 3 and 4; see Ottenwalder, 1991, for complete measurements of these specimens), thus providing a better idea of the range of variation present in that species. One complete and one partial fossil femur from Cueva Paredones (Table 4) are within the range of variation of *S. cubanus* in most measurements, whereas the three femora referred to *S. arredondo*i are from 20% (OA 301E and OA 2943) to 30% (USNM 299480) larger than *S. cubanus*. Similarly, the three humeri of *S. arredondo*i, two from Cueva Paredones and one from Caverna de Pío Domingo, average 15–20% larger than *S. cubanus* in most measurements (Table 3).

Certain insectivores, including shrew tenrecs of the genus *Microgale* (see MacPhee, 1987), exhibit a wide range of intraspecific variation in body size. Ottenwalder (1991) presented a detailed statistical analysis of geographic and non-geographic (age, sexual, individual) variation in the two living species of *Solenodon*. Measurements of the available sample of Recent *S. cubanus* (tables 1–4; Ottenwalder, 1991) demonstrate that the type skull and postcranials here referred to *S. arredondo*i are well outside the range of variation in the modern species, and do not represent exceptionally large individuals of *S. cubanus*.

Etymology.—Named in honor of our colleague Oscar Arredondo for his outstanding contributions to the vertebrate paleontology of Cuba. Sr. Arredondo was also the first paleontologist to recognize the existence of this large extinct species of *Solenodon*.

Comparative material examined.—*Solenodon cubanus* (Recent), Cuba: five skulls, two with postcranial skeletons (USNM); five skulls, four with postcranial skeletons (IES/ACC); four skulls (MCZ).

Solenodon cubanus (fossil): IES/ACC P-2325/3645, anterior portion of skull with right P¹–P², M¹; IES/ACC P-621, left humerus; IES/ACC P-620, left femur; IES/ACC P-2599/3678, partial left femur, all from Cueva Paredones, La Habana Province, Cuba (Ottenwalder, 1991).

OA uncatalogued, nearly complete skull with right I¹, C¹, P¹, P², P⁴, M¹, M² and left I¹, C¹, P¹, M². Cueva del Túnel, 3 km SE of La Salud, La Habana Province. Collected by Oscar Arredondo and Noel González, 8 August 1971 (Acevedo et al., 1972; Ottenwalder, 1991).

Solenodon cubanus (archaeological specimens): OA uncatalogued (field #35), anterior portion of skull with right P¹ and left P⁴. Cueva de José Brea, Sierra de Pan de Azúcar, Pinar de Río Province, Cuba. Collected 6–7 November 1949 by Oscar Arredondo (Aguayo, 1950; Arredondo, 1955, 1970; Ottenwalder, 1991).

IES/ACC uncatalogued, anterior portion of skull with right P¹, M¹ and left P¹–P². Los Negros, 25 km south of Baire, Santiago de Cuba Province, Cuba. Collected 19 March 1976 by Ulises Feria Bencosme (Ottenwalder, 1991).

Solenodon marcanoi (fossil): UF 128162, complete skull, Trouing Marassa, La Visite, Haiti; UF 125174, partial skull and partial associated skeleton, Trouing Carfinéyis, Formon, Haiti; UF 128163, 128180, partial skulls, Trouing Jeremie, Formon, Haiti. For a complete list of specimens of *S. marcanoi* see Ottenwalder (1991).

Solenodon paradoxus (Recent), Hispaniola: 65 skulls, most with postcranial skeletons (JAO); 32 skulls, many with complete or partial skeletons (UF).

DISCUSSION

Age and associated vertebrate fauna.—The age of the holotype skull and other fossils of *Solenodon arredondo* from Cueva Paredones is unclear, as is the age of the fossils of this species from Abra de Andrés and Caverna de Pío Domingo. No radiocarbon dates are available for any of these three localities, and as a consequence faunal associations provide the only clues to the age of the fossils. Arredondo (1976, table 1) provided a list of the associated fossil vertebrates identified from two of the three known localities for *S. arredondo*, Cueva Paredones (type locality) and Caverna de Pío Domingo. Extinct vertebrates from Cueva Paredones include: the land tortoise *Geochelone cubensis*, the condor *Antillovultur varonai*, the large eagle *Aquila borra*, the extinct owls *Pulsatrix arredondo* and *Tyto noeli*, the giant flightless owl *Ornimegalonyx oteroi*, two species of the small shrew-like insectivore *Nesophontes*, at least five species of small megalonychid ground sloths (*Miocnus antillensis*, *Neocnus gliriformis*, two species of *Mesocnus*, and *Megalocnus rodens*), two species of the echimyid rodent *Boromys*, and as many as five species of capromyid rodents. Numerous specimens of *Solenodon cubanus* were also present in fossil deposits in Cueva Paredones. Manuel Iturralde generously provided us with a sketch map of Cueva Paredones indicating where certain fossils had been found. In April 1991, Iturralde collected a proximal humerus of *S. arredondo* (MNHNC uncatalogued) about 350 m from the cave entrance and 180 m beyond the Salón del Pozo, a gallery known for the large number of fossils collected there. Except for this humerus, the specific locality within Cueva Paredones where the type skull and remaining fossils of *S. arredondo* were collected is unknown.

The associated vertebrate fauna from Caverna de Pío Domingo includes *Ornimegalonyx oteroi*, *Nesophontes micrus*, four species of megalonychid sloths (*Miocnus antillensis*, *Neocnus gliriformis*, *Mesocnus torrei*, and *Megalocnus rodens*), two species of *Boromys*, and four species of *Capromys* (Arredondo, 1976). Morgan et al. (1980) discussed the vertebrate fauna associated with the giant *Solenodon* femur from Abra de Andrés, which included four extinct species, three species of megalonychid sloths and the capromyid rodent *Geocapromys columbianus*. Arredondo (1976) also listed *Ornimegalonyx oteroi* from the Sierra de Anafe, Guanajay, presumably from this same site.

The three localities that have produced *Solenodon arredondo* have similar associated faunas, including *Ornimegalonyx*, as many as five species of megalonychid sloths, and a variety of capromyid and echimyid rodents. These faunas include numerous extinct species, as well as several extinct genera. Although not conclusive, the abundance of extinct taxa would certainly indicate a Late Quaternary age (late Pleistocene or early Holocene) for these three sites. It is difficult to separate late Pleistocene and early Holocene vertebrate faunas from the West Indies (Morgan and Woods, 1986). An abundance of extinct species and lack of evidence of humans characterize most Antillean vertebrate faunas older than about 4500 yBP, the earliest record of Amerindian peoples in the West Indies (Rouse and Allaire, 1978). The reason for the extinction of *S. arredondo* is unknown, but it is certainly not inconceivable that its disappearance was caused by humans. There is as yet no evidence that the Amerindian inhabitants of Cuba hunted *S. arredondo*. Habitat destruction and predation by dogs, which were introduced into Cuba by pre-Columbian peoples, are more likely explanations for the extinction of the giant Cuban *Solenodon*.

Distribution.—The three known fossil sites for *Solenodon arredondo* are all located in western Cuba in La Habana and Pinar del Río Provinces. Cueva Paredones is located near the town of Ceiba del Agua in La Habana Province and is only about 10 km south of the first published site for this species, Abra de Andrés in the Sierra de Anafe just north of the town of Guanajay (Morgan et al., 1980). The third site, Caverna de Pío Domingo, is located near the town of Sumidero in Pinar de Río Province about 120 km southwest of the other two sites. The giant *Solenodon* is very uncommon, having been identified from only three sites out of a total of several hundred Late Quaternary fossil localities throughout Cuba. Based on the fossil record as currently known, *S. arredondo* may have been restricted to western Cuba.

The Cuban solenodon, *Solenodon cubanus*, still survives in a rather limited area of southeastern Cuba. The historical distribution of *S. cubanus* includes localities in the provinces of Holguín, Granma, Santiago de Cuba, and Guantánamo, all of which were formerly included in Oriente Province (Varona, 1983; Eisenberg and González, 1985; Abreu et al., 1990; Ottenwalder, 1991). *S. cubanus* was rather widely distributed throughout Cuba in pre-Columbian times, particularly at the eastern and western ends of the island. Fossil and archaeological material of *S. cubanus* is known from more than 15 localities in Cuba, including specimens from the provinces of Pinar del Río, La Habana, Matanzas, Camaguey, Holguín, Santiago de Cuba, and Guantánamo (Ottenwalder, 1991). The disappearance of *S. cubanus* from most of its former range in Cuba probably can be attributed to human-related activities, including habitat destruction and predation by introduced cats and dogs.

Paleoecology.—The possible ecological role of the giant Cuban *Solenodon* was discussed by Morgan et al. (1980). The living species of *Solenodon*, *S. cubanus* and *S. paradoxus*, are rather unspecialized predators, feeding on a wide variety of invertebrate and vertebrate prey, including insects, land crabs, land snails, frogs, lizards, snakes, and bird eggs (Varona, 1983; Eisenberg and González, 1985; Ottenwalder, 1985; Abreu et al., 1990; Ottenwalder, 1991). True mammalian carnivores (i.e., members of the order Carnivora) are absent from both Recent and Late Quaternary faunas in the West Indies, disregarding the supposed Cuban fossil canids *Cubacyon transversidens* (Arredondo and Varona, 1974) and *Indocyon caribensis* (Arredondo, 1981), which were almost certainly Amerindian dogs.

The majority of carnivorous niches in Cuba are now filled by nonmammalian predators. The largest native terrestrial vertebrate carnivores in Cuba are the boa *Epicrates angulifer*, several species of raptorial birds, and *Solenodon cubanus*.

Many more large predators occurred in Cuba during the Late Quaternary, including the gigantic flightless owl, *Ornimegalonyx oteroi*, two species of very large barn owls, *Tyto noeli* and *T. riveroi*, the large eagle *Aquila borraasi* (Olson and Hilgartner, 1982, suggested that this species may actually be the same as the gigantic hawk *Titanohierax gloveralleni*), and *Solenodon arredondo*i. There were more species of mammalian prey in Cuba during the Late Quaternary as well. In addition to the four species of the capromyid rodent *Capromys* that still inhabit the Cuban mainland, the Late Quaternary terrestrial mammalian fauna of Cuba was composed of up to five species of small megalonychid ground sloths, several species of the shrew-like *Nesophontes*, two species of primates, two species of small echimyid rodents, and as many as ten species of capromyid rodents. The quoted figures for sloths and capromyid rodents are considerably less than the number of species actually described from Cuba (see lists in Varona, 1974; Morgan and Woods, 1986; Woods, 1989a), but probably more accurately reflect the real species diversity of these groups. However, most of these mammals were larger in body size than the giant *Solenodon*, and thus probably would not have constituted potential prey items. Among the mammals listed, only *Nesophontes* and a few species of rodents, including the two echimyids and several of the capromyids, would have been smaller than *S. arredondo*i.

In most cranial and postcranial measurements, *Solenodon arredondo*i is considerably larger than either of the two extant species of *Solenodon* (tables 1–4; Ottenwalder, 1991), and was thus among the largest known members of the Insectivora, living or extinct. Maximum weights and head–body lengths of the two living species of *Solenodon* (after Ottenwalder, 1991) are 800 g and 360 mm for *S. cubanus* and 1100 g and 390 mm for *S. paradoxus*. By very rough extrapolation from linear dimensions, *S. arredondo*i probably would have weighed from 1500 to 2000 g and would have had a head–body length from 450 to 550 mm. In addition to *S. cubanus* and *S. paradoxus*, the largest living members of the Insectivora are (maximum weights and head–body lengths after Eisenberg, 1981): the tenrec *Tenrec ecaudatus* (2400 g, 390 mm); the moonrat *Echinosorex gymnurus* (1400 g, 350 mm); the European hedgehog *Erinaceus europaeus* (1100 g, 300 mm); and the giant otter shrew *Potamogale velox* (ca. 1000 g, 350 mm).

The largest known insectivore was the enormous erinaceid, *Deinogalerix koenigswaldi*, from the Miocene of Italy, which had a skull 210 mm in length (Freudenthal, 1972). Comparative measurements (in mm) of *Solenodon arredondo*i and *D. koenigswaldi* (measurements in parentheses from Freudenthal, 1972) demonstrate that *Deinogalerix* was nearly twice as large: length from anterior edge of skull to posterior edge of palate, 51 (129); maximum length of humerus, 56 (103); maximum length of femur, 66 (114). The Gargano Peninsula of Italy, where *Deinogalerix* was discovered, was apparently an island in the Miocene. Furthermore, the vertebrate fauna associated with *Deinogalerix* contained several large raptorial birds, but no terrestrial Carnivora (Freudenthal, 1972). It is probably no coincidence that *S. arredondo*i and *D. koenigswaldi* both evolved on islands that were virtually devoid of other terrestrial mammalian predators (Freudenthal, 1972; Morgan et al., 1980).

Remarkable new species of Quaternary vertebrates, such as the giant *Solenodon*, continue to be discovered in the Greater Antilles, despite the fact that these islands have been extensively explored for fossils since early in this century. Perhaps the most spectacular new discovery of a West Indian fossil is the skull of a new genus

and species of extinct howler monkey, *Paralouatta varonai*, recently described from a cave in Pinar del Río Province in western Cuba (Rivero and Arredondo, 1991). Several other new, but so far unnamed, taxa of primates have been reported within the past six years from Jamaica and Hispaniola (Ford and Morgan, 1986; Ford, 1990; MacPhee and Fleagle, 1991). Woods (1989b) described *Rhizoplagiodontia lemkei*, a new genus and species of primitive capromyid rodent with rooted teeth, from several fossil deposits on the southern peninsula of Haiti. Fossils from two separate Quaternary localities in Cuba proved to belong to a bird similar to the genus *Scytalopus*, a member of a family of primitive, weak-flying passerines that are now restricted to southernmost Central America and South America (Olson and Kurochkin, 1987). These and other recent discoveries provide strong evidence that the Caribbean Quaternary vertebrate fauna is still incompletely known. Continued paleontological exploration in the West Indies will surely yield further unexpected finds.

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